THE RETINA AND OPTIC NERVE

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CHAPTER CONTENTS

INTRODUCTION

The retina forms the most inner layer of the eyeball, and functions to convert light energy into neural signals. It is bounded internally by the vitreous body and externally by Bruch's membrane of the choroid. The retina as a whole consists of the retinal pigment epithelium (RPE), specialized epithelial cells that are important for maintaining the integrity of photoreceptors, and the neural retina, which contains all of the different retinal neurons important in the first stages of vision processing. Below, we will first describe the RPE, then outline the features of the neural retina.

THE RETINAL PIGMENT EPITHELIUM

The retinal pigment epithelium (RPE) is a single layer of hexagonal shaped cells that lie between Bruch's membrane and the neural retina (Figure 6.1). RPE cells contain a high level of melanin in the apical half of each cell and are rich in transporters and metabolic pumps. The RPE plays an essential role in maintaining normal structure and integrity of the retina by performing the following five functions:

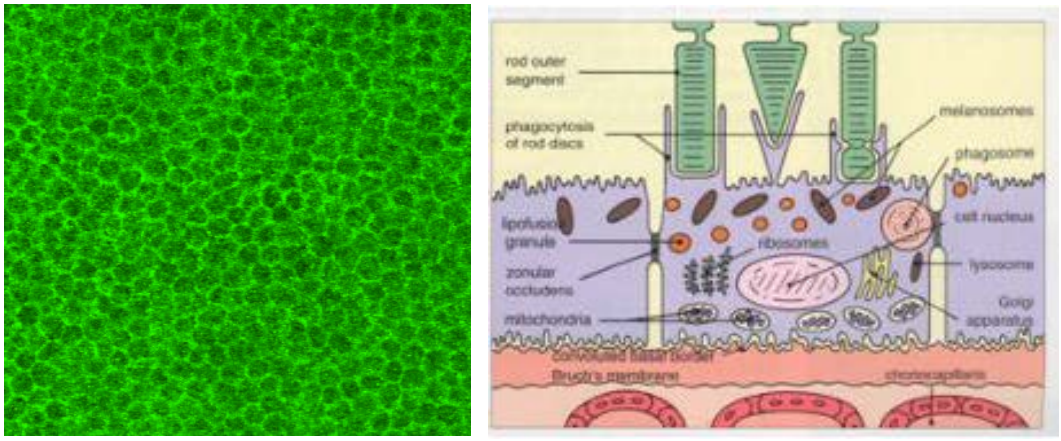

Figure 6.1: *(A) The RPE of the human retina viewed as a flatmount. The RPE consists of hexagonal shaped cells (B) schematic diagram of the contents of an RPE cell.*

i) Absorption of stray-light

Melanin granules strongly absorb visible wavelengths preventing internal reflection of stray-light within the eyeball, thus improving acuity.

ii) Active transport of metabolites

The convoluted border with Bruch's membrane increases the surface area for metabolites diffusing from the choriocapillaris and aids active excretion of waste products. A key molecule that is transported across the RPE is vitamin A, crucial for providing the chromophore of photoreceptors.

iii) Phagocytosis of photoreceptor outer segments

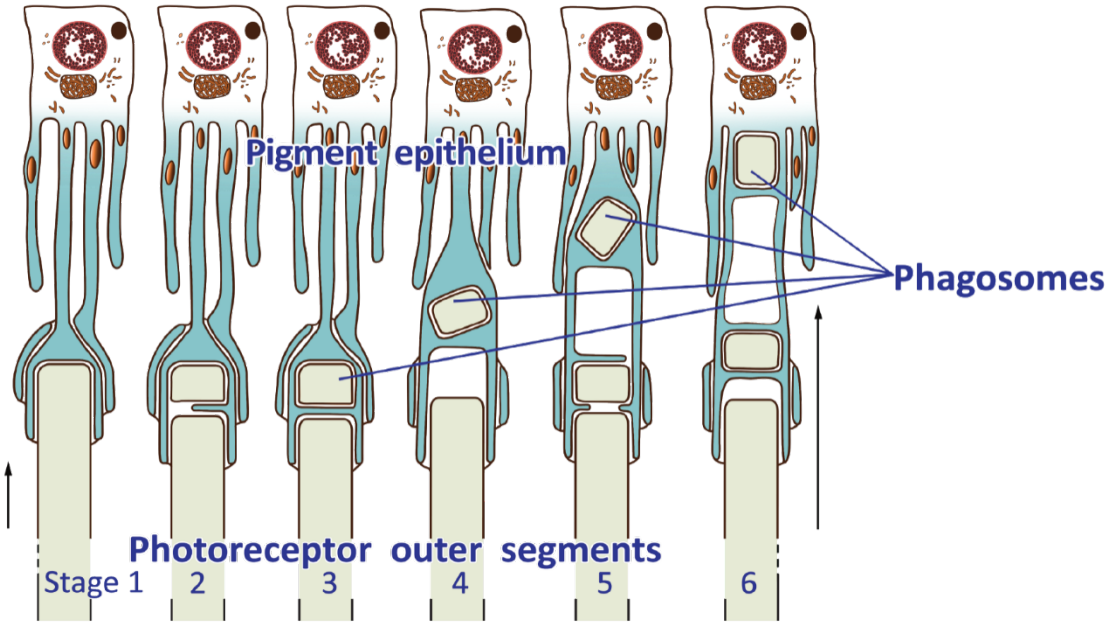

Figure 6.2: *Schematic diagram showing outer segment phagocytosis by RPE cells. Image inspired by {http://webvision.med.utah.edu/book/part-ii-anatomy-and-physiology-of-the-retina/photoreceptors/}*

Photoreceptor outer segments contain stacks of photopigment-containing discs that are constantly being formed. The RPE phagocytoses spent discs to form encapsulated particles within the RPE cells known as phagosomes (Figure 6.2). Photoreceptor outer segments bind to specific scavenger receptors such as MerTK that are expressed on the apical surface of RPE cells. Outer segments are then engulfed and degraded by the action of lysozomes to be either recycled or excreted into the choriocapillaris. With age, this process becomes less efficient and partially digested particles remain in the RPE as lipofuscin or in Bruch's membrane as drusen.

iv) Formation of blood-retinal barrier

RPE cells are joined together by a series of tight junctions. Together with the active transport through the cells, tight junctions (zonula occludens) between cells prevent free diffusion of substances from the choriocapillaris into the neural retina. This, along with the tight junctions between the endothelial cells of the retinal vasculature, forms the blood-retinal barrier.

v) Recycling of photopigment

The RPE plays an integral role in the "retinoid cycle", an important process for returning light activated photoreceptors back to their resting state. Light falling on photoreceptor outer segments initiate a conformation change in 11-cis-retinal (Figure 6.3), the chromophore that is normally bound to rhodopsin. Light causes 11-cis retinal to change to all-trans retinal, causing activation of rhodopsin and stimulating a G protein cascade that ultimately leads to closure of cGMP gated sodium channels and hyperpolarization of the membrane potential of photoreceptors. In order for the photoreceptor to return to its resting state, the all-trans retinal must be converted back to 11-cis retinal. This process takes place within RPE cells as part of the retinoid cycle. All-trans-retinal is transported to the RPE by a transport protein called interphotoreceptor retinal binding protein (IRBP) where it is isomerized via a series of steps. The final step involves transport of 11-cis retinal from the RPE cell back to the photoreceptor by IRBP.

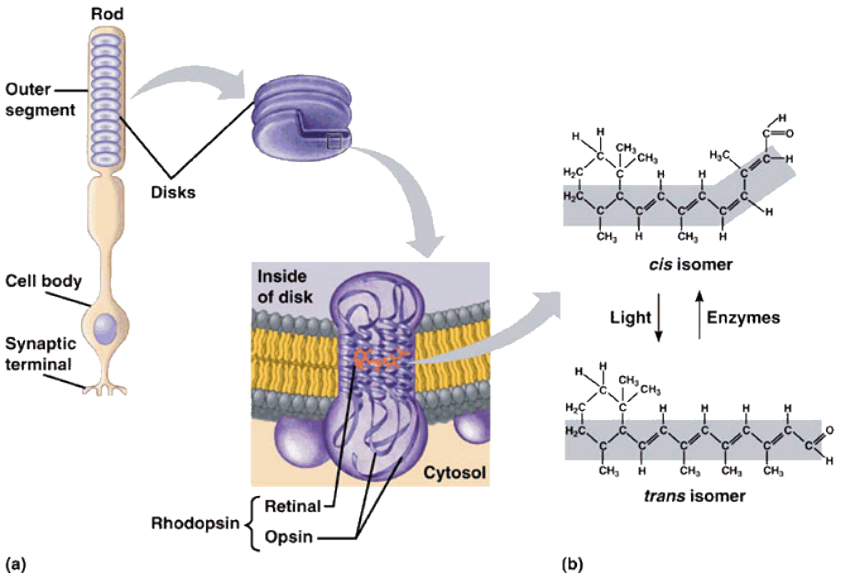

Figure 6.3 *.Schematic diagram of a photoreceptor disc. {Image from http://www.chm.bris.ac.uk/motm/retinal/retinalv.htm}*

NEURAL RETINA

The neural retina consists of alternating layers of neuronal cell bodies and synaptic layers (Figure 6.4). The following layers are in order from outer retina (i.e. closest to the choroid and sclera) to inner retina (closest to the inside of the eyeball)

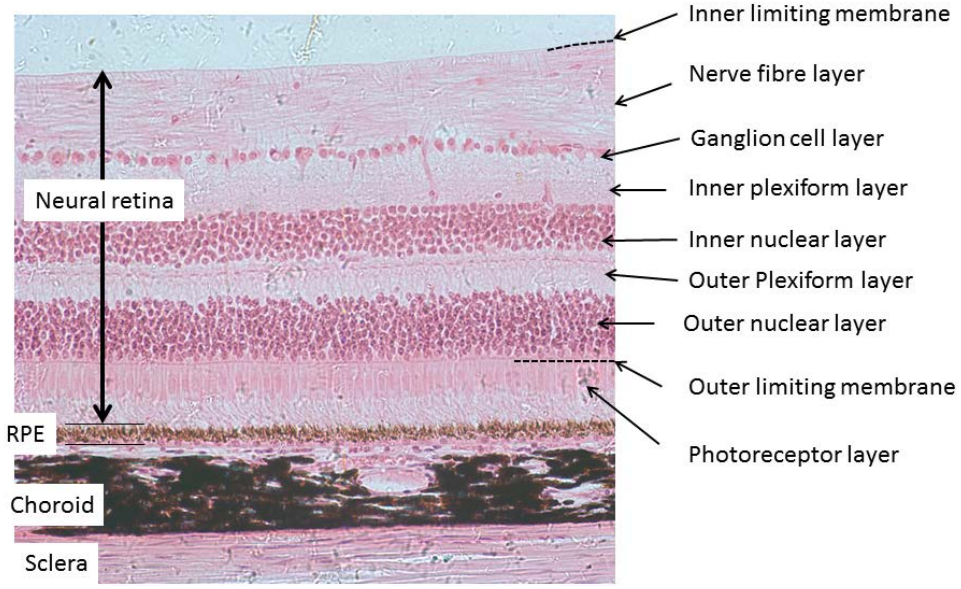

Figure 6.4*: Cross section through the retina showing the layers.*

1. Photoreceptor Layer (PRL)

It is composed of the outer and inner segments of the rods and cones. While the photoreceptor outer segment contains photopigment-laden discs and the inner segment is the ‘factory’ of the photoreceptor and is made up of the

ellipsoid (containing many mitochondria) and myoid (containing Golgi bodies and ribosomes). Photoreceptors are most numerous at fovea where acuity requirements are greatest.

2. Outer Limiting Membrane (OLM)

Not a true membrane but represents the outer limit of the glial *Muller cells* that run all the way inwards to the vitreal surface. The OLM consists of junctional contacts (zonula adherens junctions) between Muller cell processes and neighbouring photoreceptor inner segments and is thought to be important for maintaining the position of photoreceptors; in particular the contact between the outersegment and RPE cells.

3. Outer Nuclear Layer (ONL)

It contains the nuclei of the rods and cones. Cone nuclei are somewhat larger. Cones have little or no outer fibre therefore nuclei are observed closer to the OLM. This layer is thickest in fovea where many layers of nuclei can be observed.

4. Outer Plexiform Layer (OPL)

The OPL contains the synaptic terminals of photoreceptors with second order neurons (bipolar and horizontal cells). The synapses between rods and second order neurons are called spherules, whilst that of a cone is called a cone pedicle. A rod synapse, known as a spherule, contains a single “triad” of processes. A cone synaptic ending, known as a pedicle, contains up to 20 “triads”. A triad is a synaptic arrangement at the synaptic ending of a photoreceptor located at an invagination of the cone pedicle or rod spherule.

5. Inner Nuclear Layer (INL)

It consists of the nuclei of the second order neurons, i.e. the *bipolar*, *horizontal* and *amacrine* cells, along with the nuclei of the Mueller cells.

6. Inner Plexiform Layer (IPL)

It contains the processes of bipolar, amacrine and ganglion cells and their synapses.

7. Ganglion Cell Layer

It contains the nuclei of the third order neurons (ganglion cells). These cells sum the input from the bipolar and amacrine cells and pass the signal via a long axon to the higher visual centres.

8. Nerve Fibre Layer (NFL)

It is composed of the axons of the retinal ganglion cells. The axons turn at right angles from the nucleus to run in an arcuate fashion across the inner surface of retina towards the optic nerve head (Figure 6.5).

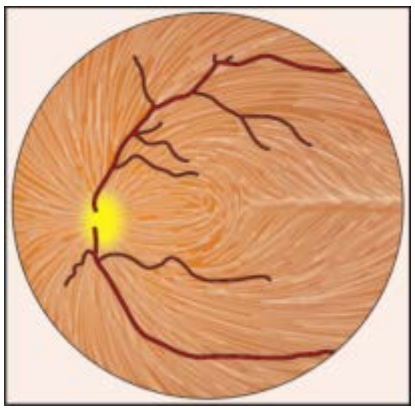

Figure 6.5: *Nerve fibre layer composed of ganglion cell axons which head for optic nerve in arcuate fashion*

9. Inner Limiting Membrane (ILM)

Again, not a true membrane, the ILM represents the terminations of the glial Müller cells. The inner surface is in contact with the vitreous.

LOCAL FEATURES AND LANDMARKS OF THE RETINA

An ophthalmoscopic view of the retinal fundus is shown in Figure 6.6. Below, the features of the retinal fundus are described in more detail.

Optic disc or optic nerve head

The optic disc is the visible portion of the optic nerve head within the eye and appears as a vertically oval yellow patch, 5 mm from fovea on the nasal side of the fundus (Figure 6.6). It is made up of the axons of the retinal ganglion cells with accompanying glial tissue and blood vessels. It varies in size between individuals (1-2 mm vertically) but larger discs, defined by a larger outer Ring of Elschnig, have more room for axons to pass through, therefore are more likely to have left-over space in the form of the optic cup. Since no photoreceptors are found on the optic disc, a physiological blind spot exists at this location.

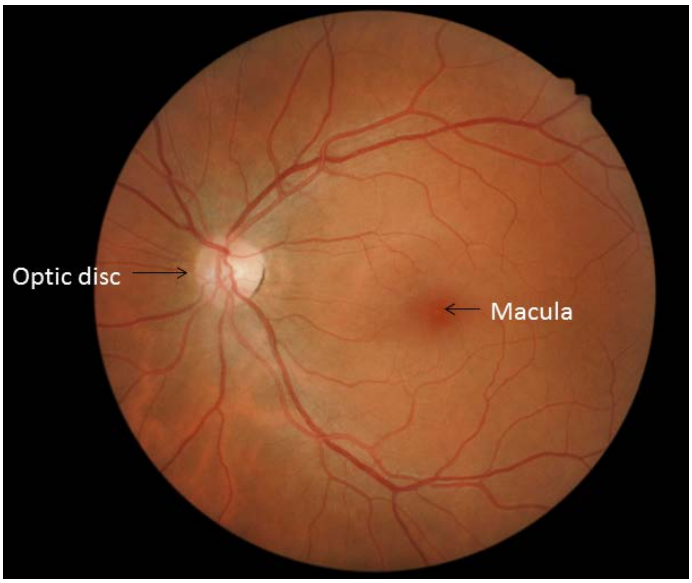

***Figure 6.6**: Retinal fundus photo showing the optic nerve head and macula.*

The optic nerve head also serves as the entrance point for the central retinal artery and vein to the eyeball. These vessels bifurcate vertically to form the superior and inferior arterial and venous arcades which supply blood to the inner retina (the outer retina is supplied from the choroid).

Macula

The macula of the central retina is 5-6 mm across, appearing darker than the rest of the retina owing to a denser RPE and the presence of yellow carotenoid pigments (lutein and zeaxanthin) mostly in the outer plexiform layer (Figure 6.7).

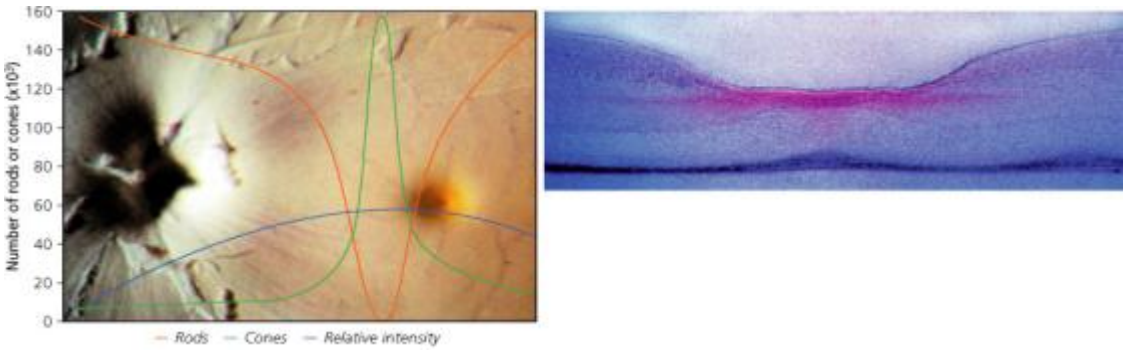

Figure 6.7: *Carotinoid pigments lutein and zeaxanthin observed in outer plexiform layer at macula*

Of significant interest in recent years, the role of the carotenoid pigments is possibly threefold:

i. *Antioxidant protection* of macula (a region of high O_2 consumption)

ii. A *filter* for (higher-energy) short-wavelength light

iii. Improvement of *image quality* by selective filtering of "blue-haze" from the environment and/or short wavelength intraocular scatter.

Fovea

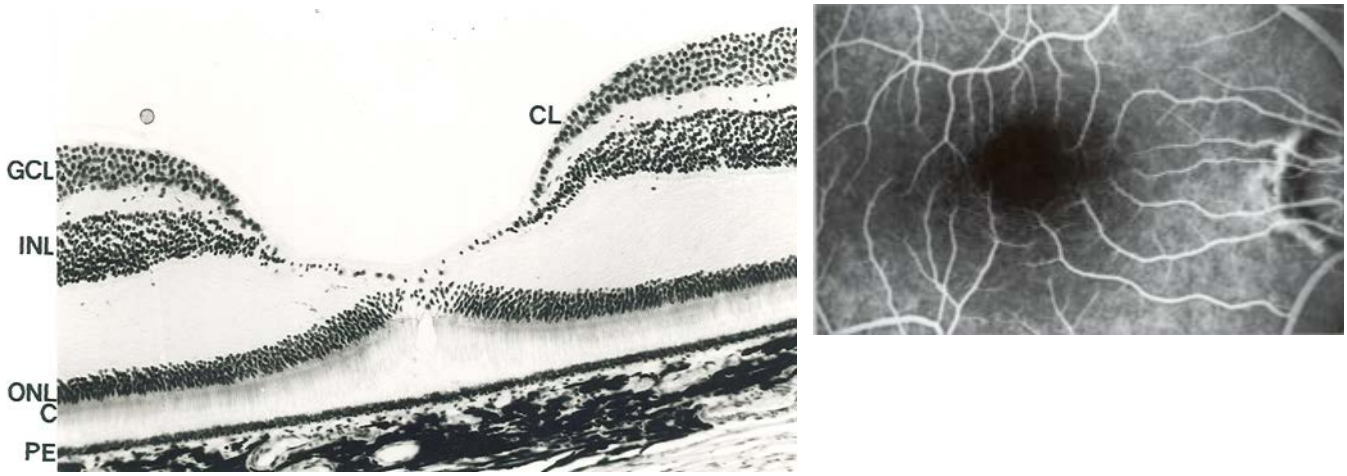

Figure 6.8: *Appearance of central foveal region of retina. Bipolar and ganglion cells displaced laterally to increase visibility of photoreceptors. Abbreviations: PE: retinal pigment epithelium; C; cone photoreceptors; ONL-outer nuclear layer; INL-inner nuclear layer; GCL-ganglion cell layer; CL-clivus (B): Image from a fluorescein angiogram of posterior pole showing greater pigmentation in the fovea and foveal avascular zone that obscures the underlying fluorescence of the choroid.*

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The fovea is the region of the central retina where visual acuity is highest. It takes the form of a depression about 1.5mm wide caused by the displacement of the higher order neurons (bipolar and ganglion cells; Figure 6.8) in order to minimize scattering of the light striking the photoreceptors. Simultaneous displacement of the retinal blood vessels from above the foveal region forms a foveal avascular zone (FAZ) (Figure 6.8) to minimize angioscotomas (photoreceptor obscuration by blood vessels) in this region of high acuity. Deviated photoreceptor fibres are observed in the fovea as *Henle's fibre layer* (Figure 6.9). Henle's fiber layer is the equivalent of the outer plexiform layer in the macular region.

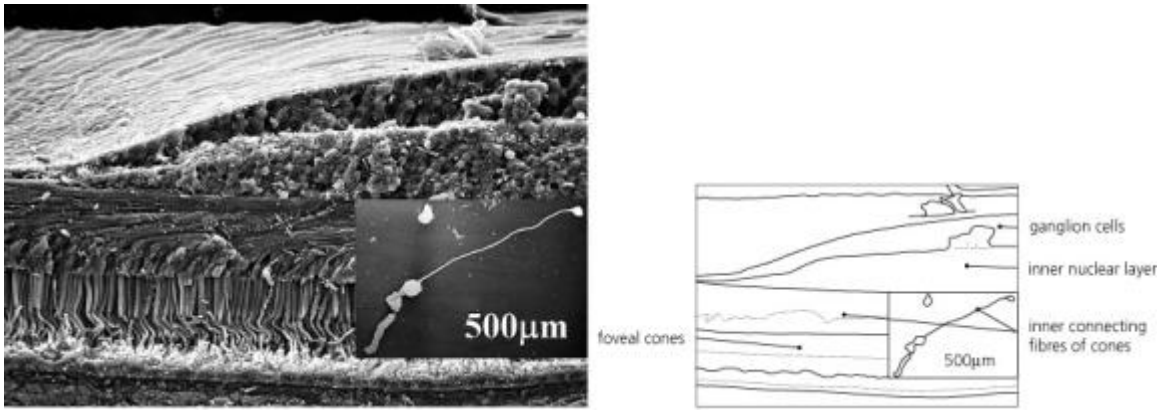

Figure 6.9: *Henle's fibre layer formed from fibres of photoreceptors near fovea.*

Foveola

It is at the bottom of foveal pit, about 0.4 mm across.

Ora Serrata

Named for its irregular jagged (serrated) appearance, the ora serrata is the anterior peripheral junction between the neural retina and the ciliary body (Figure 6.10). The serrations are normally present only on the nasal side of the eye. On the temporal side, the junction between peripheral retina and the posterior margin of the ciliary body is commonly a straight line.

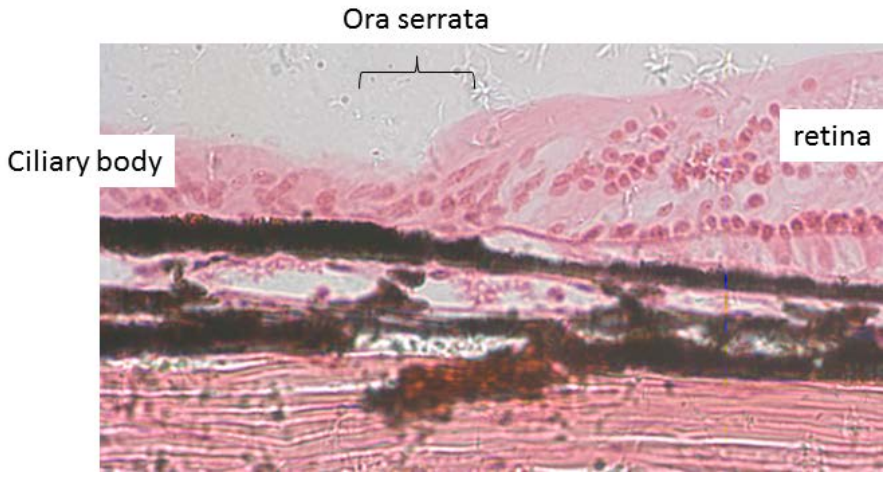

Figure 6.10*: Vertical section through the ora serrata. On the right of the picture, the neural retina can be seen. On the left, the pars plana of the ciliary body.*

CELL TYPES AND NEURAL CONNECTIVITY WITHIN THE RETINA

The main circuit by which light information is converted to a neural signal and then passed through the retina involves photoreceptors communicating with bipolar cells which in turn communicate with ganglion cells, the principal output neurons of the retina (Figure 6.11). This circuit is referred to as the retinal "through" pathway. Modulation of this basic retinal through pathway occurs in the outer retina by the lateral neurons, the horizontal cells, and in the inner retina by amacrine cells. Thus, horizontal and amacrine cells form the lateral interactions in the retina.

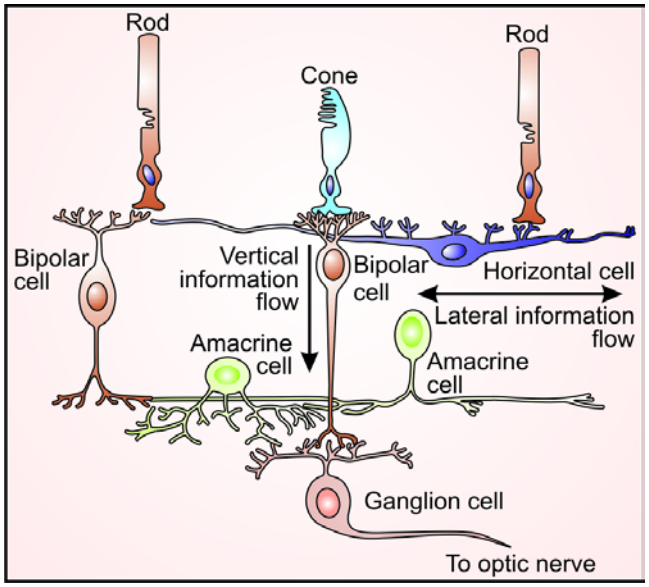

***Figure 6.11**: The main circuits for mediating vision. The through retinal pathway involves cones synapsing with bipolar cells which in turn synapse with ganglion cells. Horizontal and amacrine cells form the lateral elements for modulating the main retinal circuit.*

Photoreceptors:

There are two basic types of photoreceptor in the human retina, the *rods* and *cones*, that mediate scotopic (night-time) and photopic (daylight) vision respectively. In the human retina there are far more rods than cones, with a ratio of 20 rods for every cone. The name rod or cone comes from the shape of the outer-segment, which in rods is long and cylindrical, whilst in cones, is cone shaped across most the retina with the exception of the fovea.

There are three different cone types, being maximally sensitive in either the red, green or blue regions of the spectrum. There are around 120 million photoreceptors in the retina and these in turn connect with around 10 million second order neurons (bipolar cells) which then connect with around 1 million third order neurons (ganglion cells). There is thus a process of “convergence” over most of the retina, the exception being the fovea where there is a ‘one-to-one-to-one’ connection between photoreceptors, bipolar cells and ganglion cells in order to ensure high resolution.

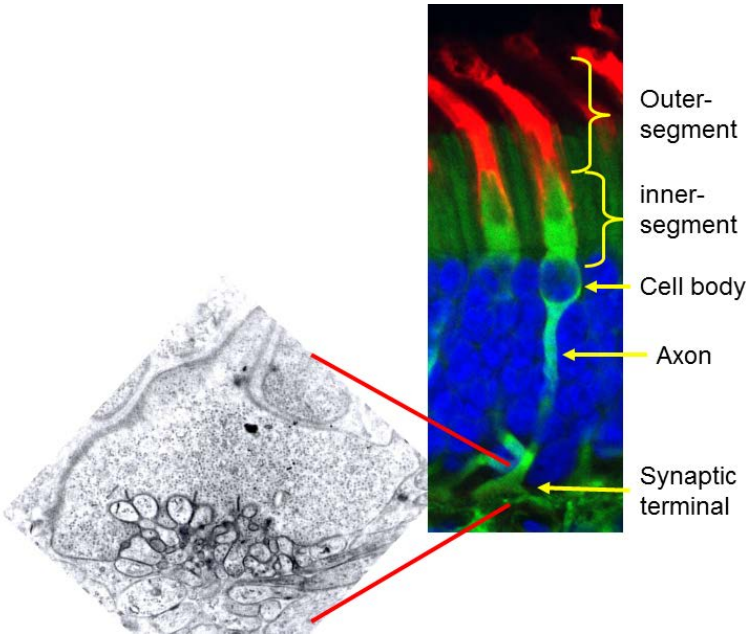

***Figure 6.12**: A cone photoreceptor showing the different cellular compartments*

The structure of a photoreceptor is shown in Figure 6.12. The outer segment, found closest to the RPE, contains many photopigment containing discs. The inner segment houses essential organelles such as mitochondria and golgi apparatus. The cell body is located within the ONL. An axon extends from the cell body and forms a synaptic terminal within the OPL. Synapses in the OPL are referred to as triads because they involve communication between three neuronal processes-a photoreceptor terminal communicates with a bipolar cell process and two horizontal cell processes. The terminals of cones are called pedicles, whilst those of rods are called spherules.

The photopigment is a transmembrane protein that undergoes a conformational change when it absorbs a photon of visible light. Rhodopsin is the photopigment found in rods, and cone-opsins are the photopigments expressed in cones. Each pigment molecule is attached to a vitamin A derivative, called retinal. Retinal acts a bit like the antenna on a television. It is the component that captures photons, thereby triggering the chain of events that is **phototransduction**. Photoreceptors do not generate action potentials (because they do not have axons). Instead their terminals release neurotransmitter more or less continuously according to their membrane potential. The more depolarized they are the more transmitter they release; when hyperpolarized they release less glutamate.

A curious feature of photoreceptors is that they are depolarized when in the dark. Incoming light causes photoreceptors to hyperpolarize and release less neurotransmitter. Thus they certainly respond to alterations in illumination but it is somewhat misleading to say their neural response is stimulated by light.

Briefly, it works like this. The cell remains depolarized while sodium channels in the outer segment are open (Na+ influx). When retinal is energized by light it changes configuration and the rhodopsin becomes activated. This leads to enzymatic reduction of intracellular cyclic guanosine monophosphate (cGMP) levels. Since many of the sodium channels are cGMP-gated, they close and the cell becomes more polarized. As a result its terminals release less neurotransmitter.

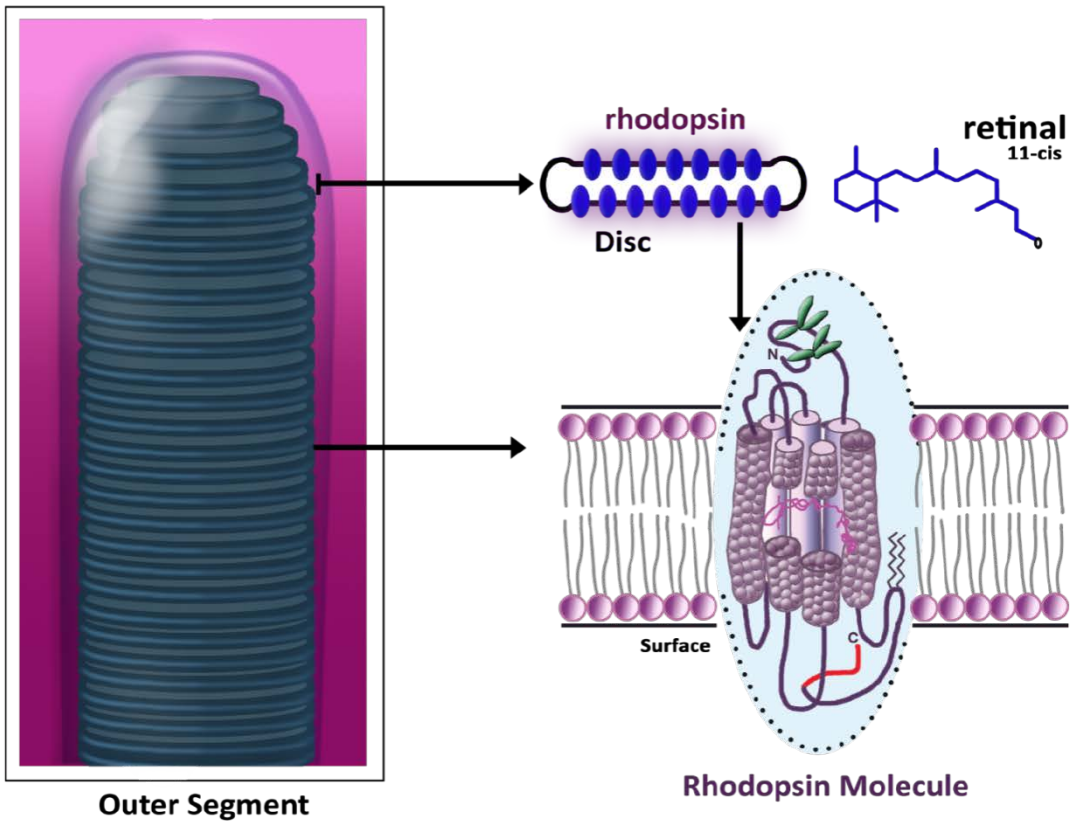

Figure 6.13: *A rod outersegment showing discs. Each disc contains the photopigment, rhodopsin.*

Phototransduction: to understand the molecular details we will focus on rhodopsin. The photopigment itself is not directly connected to any ion channel. The retinal is near the centre, surrounded by 7 protein domains. In the dark, photoreceptors are depolarized because cGMP gated sodium channels that reside within the photoreceptor outersegment membrane are open allowing influx of sodium ions. The influx of sodium ions results in a membrane potential of approximately -40mV.

When a photon of light hits a photoreceptor outersegment, there is a conformational change in 11-cis-retinal, the chromophore attached to rhodopsin. This conformational change from 11-cis-retinal to all-trans retinal activates a G-protein cascade. The steps include:

i) 11-cis-retinal to all trans-retinal and activation of rhodopsin
ii) Activation of transducin
iii) Activation of phosphodiesterase
iv) Breakdown of cGMP by phosphodiesterase.
v) Closure of sodium channels.
vi) Reduction in sodium influx into the photoreceptor outer segment and consequently hyperpolarization of the membrane potential

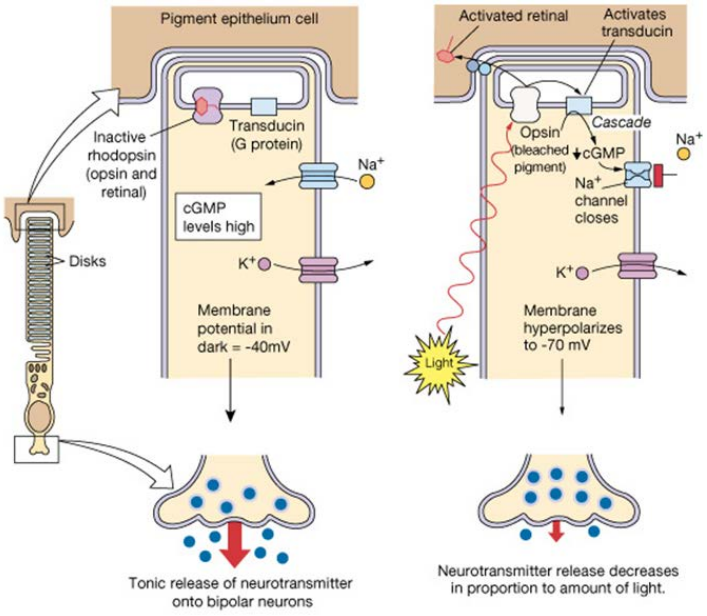

***Figure6.14**: schematic of phototransduction: Image from http://faculty.pasadena.edu/dkwon/chap10_C/chap%2010%20part%20C_files/textmostly/slide19.html*

Bipolar cells are the main second order neurons (Figure 6.15). As the name suggests they comprise of a cell body with two processes that project from the cell body (i.e. they are bipolar in shape). Bipolar cells receive input from photoreceptors within the OPL, and provide synaptic input to both ganglion cells and amacrine cells. There are at least 10 morphologically distinct types of bipolar cells in the human retina; 9 that receive information from cones, and one that receives input solely from rods. Bipolar cells respond to light falling their receptive field by either depolarizing to light (ON bipolar cells) or hyperpolarizing to light (OFF bipolar cells). They release the neurotransmitter, glutamate, in a graded fashion, depending on the membrane potential change.

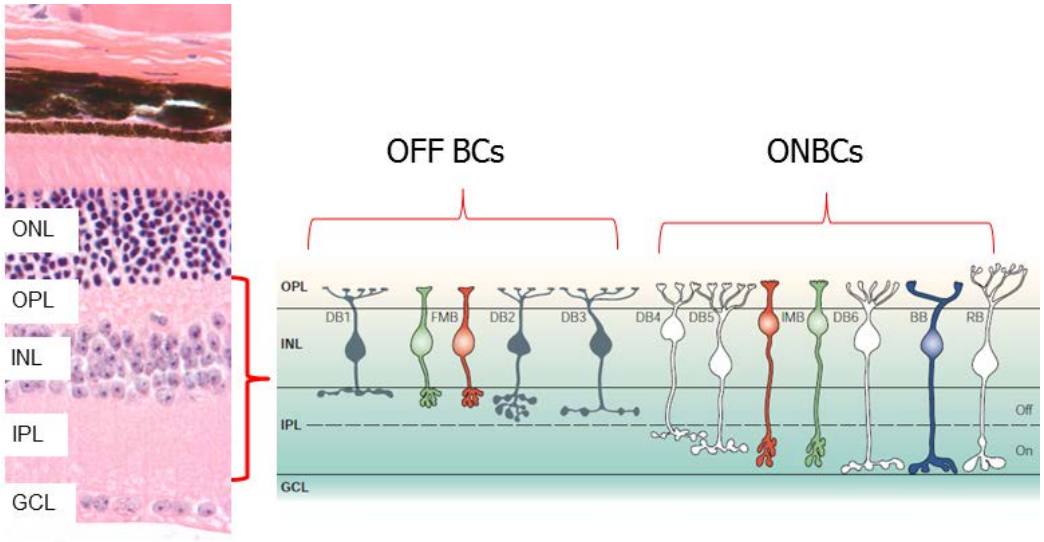

***Figure 6.15**: Different types of bipolar cells in the human retina.*

The synapse between bipolar cells and third order neurons, amacrine and ganglion cells is called a dyad because the bipolar cell process communicates with two neural elements. This is shown in the electron micrograph in Figure 6.16.

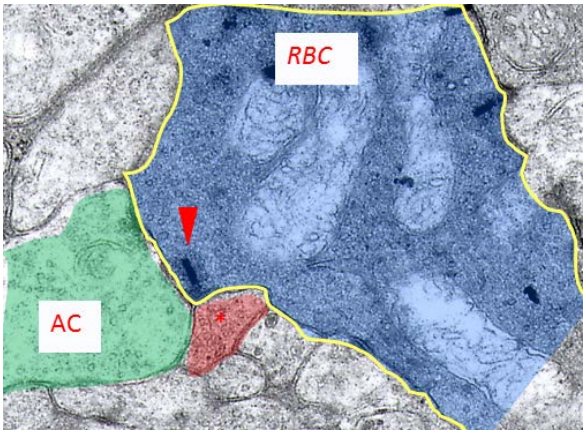

***Figure 6.16**: a Dyad synapse in the IPL. In this image, a rod bipolar cell terminal is shown in blue. The release neurotransmitter occurs at the synaptic ribbon (indicated by the red arrowhead). There are two postsynaptic neural elements shown in green and red. Usually one element is an amacrine cell (AC; green) process, whilst the other is a ganglion cell process (red)*

Although photoreceptors all release glutamate as their neurotransmitter, the effects of glutamate on bipolar cells varies according to the type of bipolar cells. ON bipolar cells are activated (depolarized) by photoreceptors' response to light, whereas OFF bipolar cells are inhibited (hyperpolarized). At the cellular level, the response of a bipolar cell to glutamate depends on the glutamate receptor that is expressed by the cell. In the case of ON bipolar cells, mGluR6 is the receptor expressed, whilst ionotropic glutamate receptors including AMPA and kainite receptors are the glutamate receptors expressed by OFF bipolar cells. It is because of the actions of glutamate on these two different types of glutamate receptors that bipolar cells either depolarize or hyperpolarize. This creates parallel processing of visual information at the very first synapse in the retina, between photoreceptors and bipolar cells.

Horizontal cells

Horizontal cells spread their dendrites horizontally across the retina (Figure 6.17). They receive input from photoreceptors and also feedback back information to photoreceptors. Thus, they are crucial in modulating the retinal through pathway and in particular for providing a neural circuit important for creating the surround in a ganglion cell receptor field. Their nuclei are located in the INL at the border with the OPL.

Functionally, horizontal cells receive inputs from photoreceptors via ionotropic glutamate receptors (so a depolarized photoreceptor also depolarizes a horizontal cell). The terminals of horizontal cells release the inhibitory transmitter

GABA onto the presynaptic regions of other photoreceptors a short distance away. Thus, horizontal cells provide an important feedback mechanism that regulates the retinal through pathway.

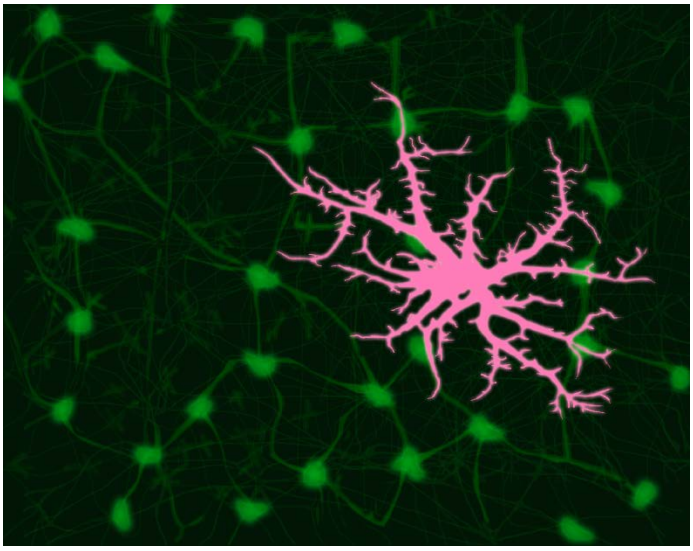

***Figure 6.17**: a horizontal cell when viewed in a retinal flatmount. These cells extend processes that contact photoreceptors (shown in green).*

Amacrine cells

Less well understood, the amacrine cells act as intermediary neurons between bipolars and the third order neurons (GC's; Figure 6.18). They possess no axons and also send their dendrites horizontally across the retina. Their nuclei are observed on the inner side of the INL. They also contribute to the centre/surround field of GC's and possibly play a role in a retinal negative feedback mechanism and adjustment of retinal sensitivity. Two well-studied amacrine cells include the AII amacrine cell, which is a crucial interneuron in the rod pathway, and the starburst amacrine cells, that are important for motion detection.

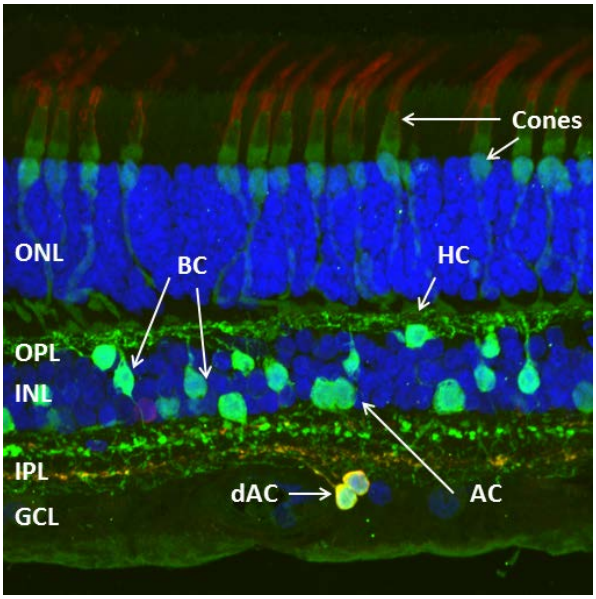

***Figure 18**: A vertical section through the retina showing the different neural types that form the INL. In green are horizontal cells (HC), a subtype of bipolar cells (BC) and two types of amacrine cells (AC, dAC). Some amacrine cells are displaced (dAC) to the ganglion cell layer.*

Ganglion cells

Ganglion cells are the output neurons of the retina and along with displaced amacrine cells, they are located in the ganglion cell layer. There are at least 20 morphologically distinct types of ganglion cells. There are several functional classes of ganglion cells including midget, parasol, bistratified and intrinsically photosensitive ganglion cells. Ganglion cells receive input from bipolar and amacrine cells within the IPL and send out a single long axon that

passes via the nerve fibre layer to the optic nerve and to high brain centres. Within the retina, ganglion cell axons are unmyelinated. However, from the level of the lamina cribosa, ganglion cells become myelinated.

Midget ganglion cell are the most numerous of the ganglion cell population and possess a small nucleus and dense small dendritic tree. Involved in high spatial resolution they are most numerous in the central retina where they may connect with only one bipolar cell and photoreceptor (zero 'convergence'). They connect mostly to the parvocellular layers of the lateral geniculate nucleus (LGN) in forebrain.

Parasol ganglion cells represent approximately 10% of the total GC cell count. With large cell nuclei and large dendritic trees, they display largely achromatic responses with fast conduction and high temporal response characteristics. They project mainly to the magnocellular layers of the LGN.

The small bistratified ganglion cell has a small cell nucleus and medium-sized but sparse dendritic tree. It is so-named because it synapses at two levels within the IPL. Conduction velocityis sluggish and projection is to the koniocellular layers of LGN.

Functionally, ganglion cells generate action potentials (sent along the optic nerves), and increase this output in response to excitation from bipolar cells. Again there are two functional classes: ON ganglion cells receive excitatory inputs from ON bipolars, and OFF ganglion cells receive excitatory inputs from OFF bipolars. This means that there are ON types of midget ganglion cells, OFF types of midget ganglion cells, ON parasol cells and so on.

Ganglion Cell Receptive Fields: The receptive field of a retinal ganglion cell is the small zone of retina in which light causes a distinct change in neural activity of that cell. Connections involving horizontal cells and also the horizontal extent of its dendrites mean that one ganglion cell is influenced by a cluster of nearby photoreceptors. Thus, there is convergent input. Moreover the route taken by signals from the surround photoreceptors differs from the more direct pathway from the centre photoreceptors.

In general, ON centre ganglion cells are depolarized and fire action potentials when a small spot of light falls on the central part of their receptive field.

Müller cells are radial glia and the main glial cell type in the retina.These cells are the support cells of the retina and are crucial for maintaining the normal function of the neurons in the retina. Müller cells have a cell body that sits in the middle of the INL, and extend processes towards the outer retina that terminate at the outer limiting membrane. In addition they project processes that terminate at the inner limiting membrane at the retina-vitreal border.

Müller cells have important function in taking up and recycling the amino acid neurotransmitters, glutamate and GABA, siphoning potassium from the extracellular space, maintaining the blood retinal barrier and also in transporting vital energy metabolites between the vasculature and neurons. More recently they have been shown to have active functions that regulate blood flow and neuronal function. In particular, glial cells are functionally active, communicating with one another by waves of intracellular calcium. Neuroactive substances (called gliotransmitters because they are released from glia and not neurons) such as glutamate or ATP can be released in response to the changes in intracellular calcium and lead to altered neural function (e.g. hyperpolarization of neighbouring ganglion cells) or changes in blood vessel calibre.

Astrocytes are the second type of glial cell that resides within the retina. They lie in the nerve fibre layer of the retina and have long processes that extend cross the retina to communicate with blood vessels. They play an important role in regulating the development of the vasculature as well as maintaining the blood retinal barrier.

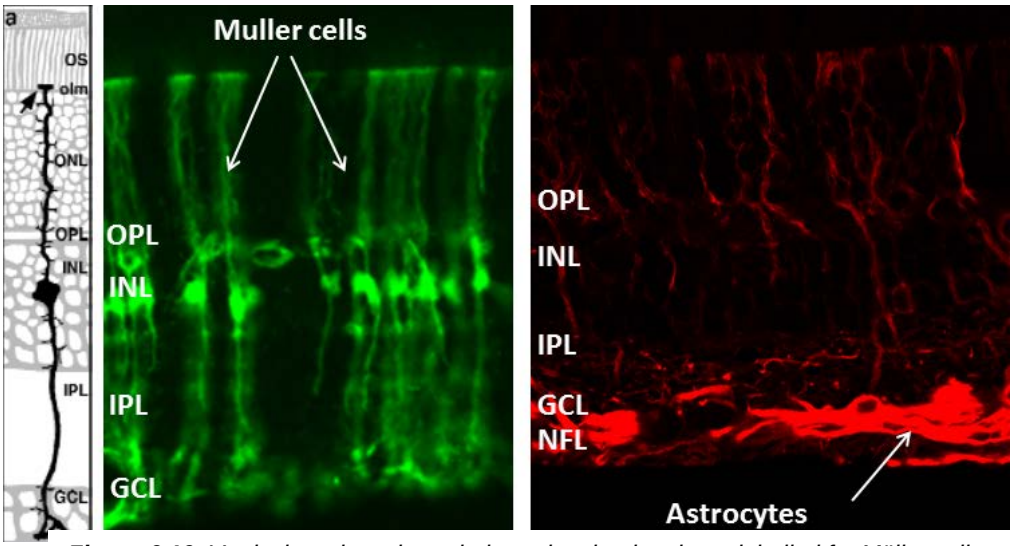

***Figure 6.19**: Vertical sections through the retina that has been labelled for Müller cells (green) or astrocytes (red).*

THE OPTIC NERVE

The optic nerve (Figure 6.20) is composed of the axons of the retinal ganglion cells and resembles the white matter of the brain. Approximately 1.2 million fibres form the optic nerve. 80-90% are of small diameter and belong to the midget class of ganglion cells.

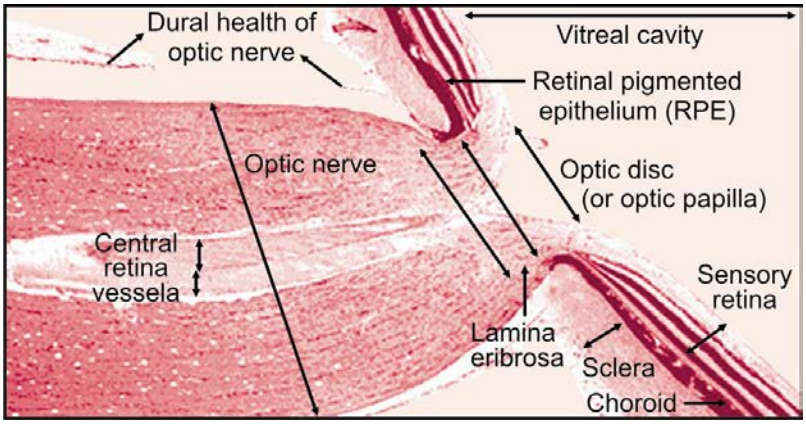

***Figure 6.20:** Cross section of optic nerve showing fibres*

Enclosed by the dura mater, arachnoid mater, subarachnoid space and vascular pia mater sheath, the optic nerve is surrounded in the orbit by orbital fat and the rectus muscles. The nerve exits the orbit by the optic canal.

The total length of the nerve is around 5cm. The portion that lies within the orbit is termed the *intraorbital* optic nerve and is approximately 25mm long.

The *optic nerve head* is that portion that lies within the scleral canal of the eyeball. It is located 15 degrees nasal to the macula and slightly above. No rods or cones are present at the nerve head which thus constitutes a *blindspot*.

The ganglion cell axons that make up the nerve fibres are unmyelinated until they reach the *lamina cribrosa* in the optic nerve head. Fibres cross in the inner retina from the ganglion cells to the optic disc in an arcuate fashion. More

peripheral fibres enter the peripheral optic nerve head. Fibres are divided into bundles within the nerve by fibrous septa. Post-laminar myelination increases the diameter of the optic nerve by more than a factor of two.

The *lamina cribrosa* (Figure 6.21) represents the scleral fibres that pass across the regions where the optic nerve enters the posterior aspect of the eyeball. It is composed of layers of porous laminae containing collagenous fibrous and elastic tissue. Around 200-400 pores are present in each lamina. The lamina acts as a support for the nerve fibres passing through to the intraorbital optic nerve.

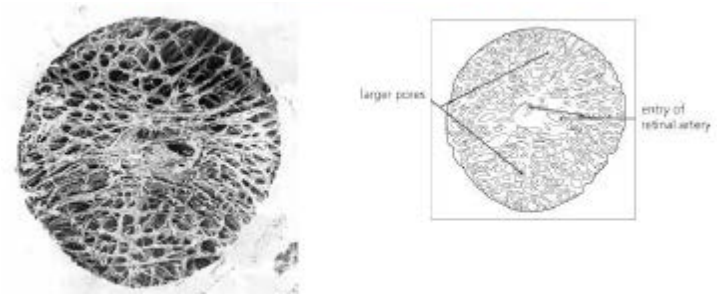

Figure 6.21: *The lamina cribrosa*

The nerve passes to the rear of the orbit and enters the optic canal in the sphenoid bone along with the ophthalmic artery. The nerve portion within the optic canal is termed the *intracanalicular* portion and extends for about 5mm. It then enters the subarachnoid space and progresses towards optic chiasm as the *intracranial* portion of the optic nerve.

VASCULAR SUPPLY TO THE RETINA AND OPTIC NERVE

The intraocular portion (ON head) is supplied by the short posterior ciliary arteries via *Circle of Zinn* (Figure 6.22). The pia mater plexus penetrates the nerve all along its length and supplies the exterior fibres within the nerve.

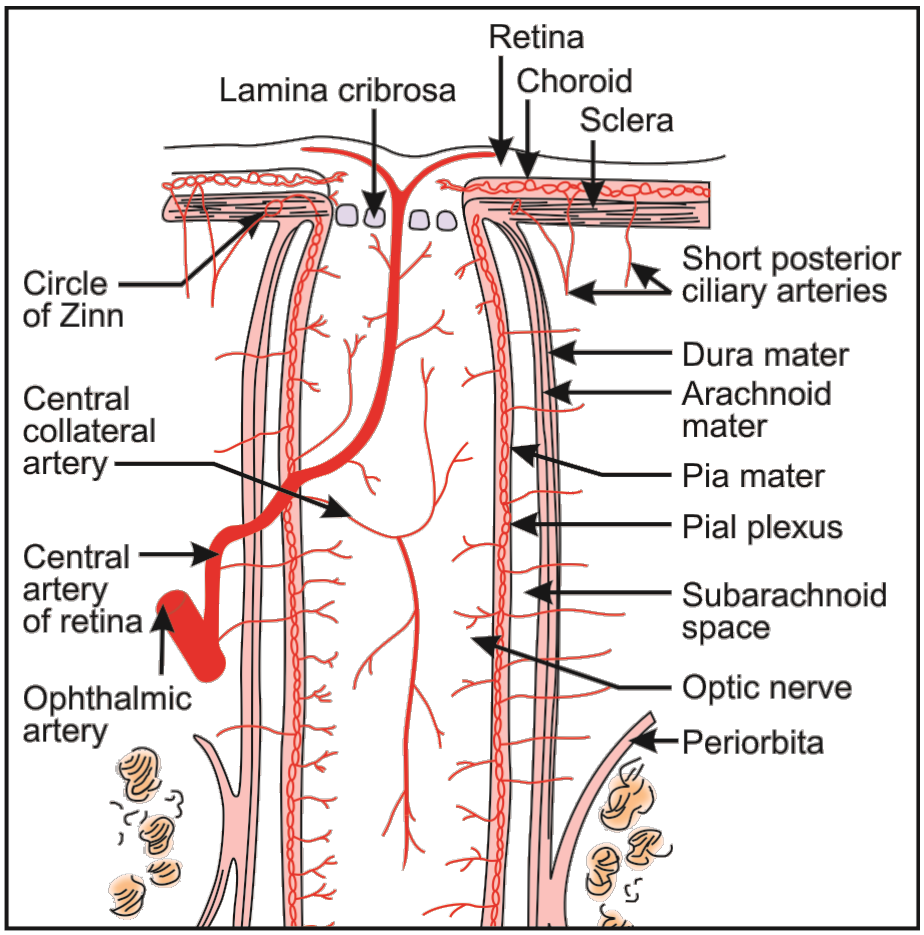

Figure 6.22: *Blood supply to optic nerve*

The central retinal artery (CRA) and vein enter the optic nerve infero-nasally about 12mm behind the globe (Figure 6.23). The artery enters anterior to the vein and both pass together anteriorly up the centre of the nerve, through the lamina cribrosa, to enter the eye through the centre of the optic nerve head. Collateral branches of the CRA supply the central fibres of the intraorbital nerve and the superficial disc surface capilliaries (minor).

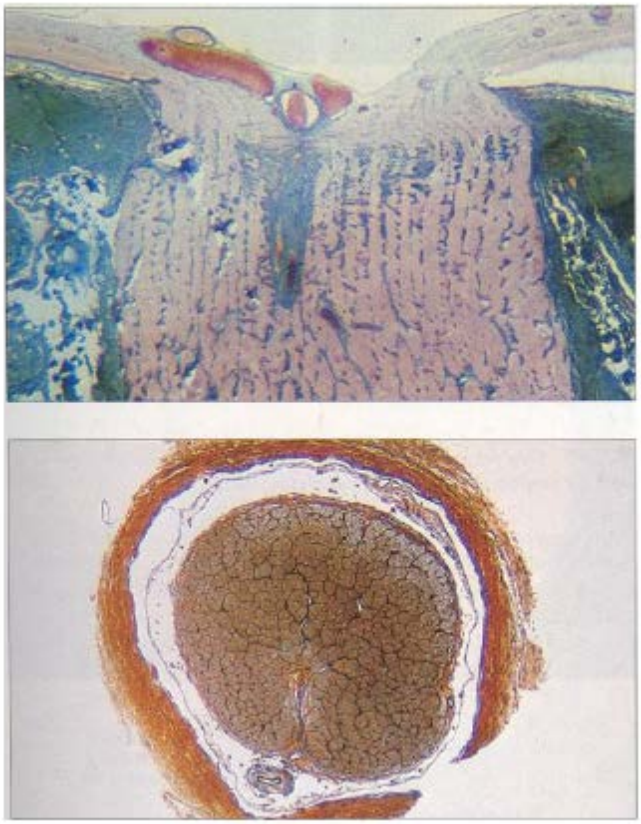

Figure 6.23: *Section through optic nerve 12mm behind globe; Central retinal artery within subarachnoid space heading towards centre of nerve*

FURTHER READING

For alternative or more detailed descriptions of different visual structures, the student may find the following books helpful.

- *Adler's Physiology of the Eye*. 11th Levin. Nilsspm. VerHoeve, Wu, Kaufman, Alm Saunders 2011.
- *Clinical Anatomy of the Visual System.* 2nded Remington, Elsevier 2005.
- *Clinical Anatomy of the Eye*. Snell and Lemp, Blackwell 1998.

Useful websites

- http://webvision.med.utah.edu/book/